The role of disturbance in dryland New Zealand: past and present

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Geoff Rogers, Susan Walker and Bill Lee

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Cover: *Muehlenbeckia astonii* and botanists at Balmoral, North Canterbury, 2001.
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The role of disturbance in dryland New Zealand: past and present

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ABSTRACT

We examine the proposition that disturbance, in the ecological sense, is necessary for persistence and recovery of rare-plant habitats in open vegetation of dry eastern New Zealand, these 'drylands' being the Level IV land environments (LENZ) east of the main axial ranges with average Penman annual water deficits of ≥ 270 mm. Local flooding and sedimentation and rare lightning-strike fire dominated the pre-settlement disturbance regime of what was a comparatively stable dry environment. Modelled vegetation reconstructions and the subfossil and pollen records depict vegetation prior to human settlement as tiered shrubland and low forest with stress- or browse-tolerant grass and herb understoreys. Grasslands per se were quite restricted below the treeline, with little evidence for seral vegetation promoting increased fire frequency over that of background levels. We suggest that herbivory and trampling by large herbivorous birds (eastern guild of moa) fostered habitats and regeneration conditions for much of the rich eastern flora of understorey grasses and forbs. In particular, the birds' feeding action and ground scarification may have promoted both clonal perpetuation and seed regeneration opportunities, strategies predominant among the 235 dryland rare species. These rare plants today inhabit a fundamentally different biome to that of pre-settlement times (no woody overstorey or matrix), competing with a guild of sward-forming grasses. The predominant pre-settlement regime of disturbance by large browsing birds, and seed dispersal and pollination by birds, bats, geckos and skinks, has been replaced by one dominated by humans and their activities, plus a mostly mammalian fauna with novel modes of herbivory and different consequences for ecosystem function. We suggest that sustained recovery of the suite of threatened dryland plants will depend upon the restoration of their habitats, as illustrated by a case study of the threatened shrub *Muehlenbeckia astonii*. A strategic review is needed to identify management actions that will facilitate the restoration of structurally complex, indigenous-dominated woody communities supporting secure populations of threatened dryland biota, including threatened fauna.

Keywords: disturbance, dryland, environment classification, eastern New Zealand, impacts of human settlement, *Muehlenbeckia astonii*, prehistoric birds, pre-settlement vegetation, shrubland, threatened plants

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1. Introduction

New Zealand's climatic pattern is profoundly shaped by the prevailing westerlies which bring moisture from the Tasman Sea, and by the main north-to-south-running axial mountain ranges of both islands, which cast long rain shadows. Eastern interior regions of both islands are considerably drier than western and coastal regions. In the drier eastern rain-shadow zones (hereafter 'drylands' or 'eastern New Zealand dryland zone'), indigenous ecosystems have been greatly modified by fire since human settlement, and by agriculture since the arrival of Europeans.

Seral grassland and shrublands now dominate those areas of the eastern dryland zone where indigenous cover remains. These communities are anthropogenically induced, and have no equivalent in the historical record (McGlone et al. 1995, 1997). Modelled predictions of species' distributions in the past suggest that there are no environmental limits to the dominance of trees and shrubs in eastern New Zealand below the regional treeline (Walker, Lee et al. 2003a, 2004a; Leathwick et al. 2004). Instead, the present-day communities arose from the suppression of previously dominant trees and shrubs by periodic fires that commenced with the arrival of humans about 750 y BP (McGlone 2001; Walker, Lee et al. 2004a). These fires were most intense and extensive in environments with low moisture availability, i.e. in those lowland rain-shadow environments lying east of the main axial ranges of both islands. Despite their human-induced origins, the seral communities of grasses, herbs and scattered shrubs that dominate the eastern rain-shadow zone today are widely regarded as the de facto natural vegetation cover (McGlone 2001). However, because they are recently created and not in equilibrium with the current climate, it is inevitable that these communities will be unstable, and continue to change in composition, structure and ecosystem function.

New Zealand environments vary considerably in the extent of remaining indigenous vegetation they contain, and in the degree of formal protection for remaining indigenous ecosystems. Most of New Zealand's remaining indigenous cover, and most public conservation land, is in wetter, upland environments (Leathwick et al. 2003). Little of the land area of the eastern New Zealand dryland zone enjoys formal ecosystem protection. Here, the combination of progressive destruction of indigenous habitats for agricultural development, and the near absence of conservation areas, has resulted in a high proportion of New Zealand's dryland plants and animals becoming threatened or at risk of extinction. There is increasing recognition that improved security of the full range of threatened species and ecosystems in New Zealand will depend largely upon making conservation gains in modified and more imminently threatened environments and ecosystems. Modified areas that were once regarded as insufficiently pristine to be important for conservation are now understood to be 'significant' (i.e. to require protection) for maintaining biodiversity, ecosystem services, landscape natural character and other attributes valued by society. Consequently, the Department of Conservation (DOC) is managing increasing areas of land in eastern New Zealand, much of it accruing from the tenure review of Crown pastoral leases.

In the last c. 150 years, seral communities (grasslands and shrublands) have been perpetuated and successionally retarded in the eastern New Zealand dryland zone by a combination of fire, pastoral use and grazing by feral mammals. However, in the future, areas managed for conservation purposes are likely to be released from pastoral use to encourage natural succession in seral communities. This is because the aim of conservation management of degraded or seral communities is to foster late successional and therefore more resilient vegetation. The persistence of rare species within seral communities will be an important component of future conservation goals for these environments, and it will be necessary to predict changes in the abundance of rare species as succession proceeds. Goals that address the persistence of individual rare species are likely to be specific to particular sites, and nested within the higher-level goals for the wider landscape (Rogers et al. 2002).

DOC has a research programme on techniques to prioritise and guide restoration of dryland ecosystems of eastern New Zealand. Several research projects have already been completed. These include examining:

- The status of and threats to Otago's saline patches (Rogers et al. 2000)
- The habitats of spring annual plants (Rogers et al. 2002)
- The woody vegetation potential of Central Otago (Walker, Lee et al. 2003a)

The eastern New Zealand dryland zone is seen as problematic for conservation management, for the following reasons:

- Scientific understanding of its pre-human vegetation and faunal composition, and the zone's potential future composition and likely future trends, remains limited in its spatial and temporal precision. Therefore, formulating coherent, persuasive and realistic conservation goals and management strategies for seral vegetation and the threatened species within it is challenging.
- There is a body of opinion that secondary succession in the absence of grazing and burning poses a threat to many of the indigenous plants and animals that currently inhabit open vegetation in eastern New Zealand. In particular, where herbivore numbers are reduced, exotic grass swards may increase in biomass and transform habitats where the persistent influence of sheep and rabbits had maintained low, open cover with much bare ground over the last c. 150 years. Exotic grass swards associated with grazing removal may exclude low-growing, grazing-avoiding, drought-tolerant indigenous plant species (including rare-plant species) that had been supported in grazed open habitats until recently. Where woody indigenous species are present, dense grass swards may reduce regeneration and spread by preventing seedling establishment. Removing some of the disturbances associated with human land use (particularly grazing) may therefore result in a net disadvantage to indigenous species rather than improving their prospects. Consequently, it has been suggested that continued grazing by stock or rabbits in dryland environments is necessary to retain indigenous species in some situations (e.g. Meurk et al. 1989).
- The fire-risk of the different types of dry seral vegetation is poorly understood, with today's ignition sources far exceeding those of pre-settlement lightning strike.

A central question that arises from the problems above is whether disturbance had a selectively advantageous role in the past. If the threatened plants of the eastern dryland zone are disturbance adapted, they may require similar disturbances in order to persist today. If so, what type of disturbance is appropriate to maintain and restore eastern dryland ecosystems, and at what frequency and intensity?

This report considers whether disturbance is an essential factor in the restoration of both matrix seral vegetation and the local habitats of threatened plants in eastern South Island. Our approach is to review the evidence for pre-settlement disturbance, and to compare this with the disturbance regimes of the post-settlement era. We have attempted to report as comprehensively as possible. Accordingly, the report is in several parts, and some sections contain considerable detail. Finally, a synthesis of our main conclusions and recommendations relating to future outcomes and supporting research is presented.

1. First, we set out to define the spatial extent, and the types and characteristics, of environments of the eastern South Island dryland zone using relevant digital environmental data layers from the wide range now available. We determine how well the full range of dryland environments is represented in protected natural areas (by DOC conservancies).
2. Having described the spatial extent and environmental context for our review, we then discuss pre-settlement and present disturbance regimes in New Zealand, and their equivalence. Drawing on reconstructions of pre-settlement vegetation, our classification of dryland environments, our field knowledge of relict vegetation and our review of pre-settlement disturbance regimes, we pragmatically propose seven broad pre-human vegetation types for dryland South Island.
3. Next, we list rare and threatened plants and their ecosystems within dry eastern New Zealand, and compare the likely pre- and post-settlement disturbance phenomena applying to each ecosystem. From this, we draw conclusions on the likely disturbance-dependence of rare plants contained within dry seral communities in eastern New Zealand.
4. We use the threatened plant *Muehlenbeckia astonii* as a case study to apply our understanding of the disturbance history of an eastern New Zealand dryland habitat. From our understanding of the disturbance and life-history attributes of *M. astonii*, we recommend habitat restoration goals as part of the species recovery plan.
5. Finally, we present a synthesis of our findings and conclusions from the review. We apply these insights to suggest appropriate biodiversity conservation goals and outcomes for dryland environments. We suggest areas of research that will be needed to support conservation management.

2. Objectives

The objectives of the study brief, and the sections of the report in which they are addressed, are listed below:

- Provide a LENZ-based analysis of the geographical range of dryland ecosystems of eastern New Zealand (Section 3).
- Summarise the climate, geology and landform characteristics of these ecosystems, and determine how well the full range of dryland environments is represented in protected natural areas (by DOC conservancies, Section 3).
- Provide a classification of pre-settlement and contemporary disturbance phenomena in New Zealand (Sections 4 & 7).
- Summarise our knowledge of successional trends within dryland seral vegetation for the various vegetation zones (Sections 5 & 6).
- Classify New Zealand's threatened and uncommon plants of dryland ecosystems into disturbance- and stasis-dependent habitats and ecosystems (Sections 8 & 9).
- Recommend methods and priorities for advancing our understanding of the effects of different disturbance agents on dryland seres or their ecological release (Section 10).
- Review and recommend methods useful for studying individual, habitat-specific, threatened plant issues in dryland ecosystems with and without successional disturbance agents (Section 10).

3. Eastern New Zealand dryland environments

3.1 INTRODUCTION

The availability of water is one of the key drivers of biological patterns at global and local scales (Woodward & Williams 1987; Leathwick et al. 2003). Low water availability is a defining feature of 'dryland' environments, which typically support biota with some degree of adaptation to moisture stress. Water availability depends upon the balance between rate of supply (usually rainfall), run-off and demand (evaporation), rather than simply upon the amount of rainfall received. Measures of rainfall alone are therefore of limited use in understanding the degree of dryness of an environment and consequent effects on the biotic pattern.

In New Zealand, landscape-scale variations in water supply are strongly influenced by the interaction of the prevailing moisture-laden, westerly winds with the geographic position of the major axial mountain ranges. Because moisture is precipitated from westerly föhn winds as they pass over the main axial ranges, the air is drier in eastern parts of New Zealand than in the west, and particularly large vapour pressure deficits occur in the lee of the highest mountain ranges. Although the westerly rain-shadow effect is important, southwesterlies and easterlies are significant sources of moisture in the east of both islands, while in the northern North Island, westerly rainfall is considerably augmented by subtropical storms from the northeast, and summer convection adds substantially to water supply in central districts. The availability of this water is determined by evaporation rates (which are highest in northern areas experiencing high solar radiation and high temperatures), by the supply of water from the soil, and the dryness of the air.

Three water balance variables have been modelled for New Zealand (Leathwick et al. 2003).

1. Average annual water deficit (deficit). This is an index of soil dryness, used to distinguish between New Zealand's driest environments, i.e. those that experience evaporation in excess of the amount of precipitation they receive. The index does not distinguish between environments that experience precipitation in excess of evaporation; these share a value of zero.

2. Average monthly water balance ratio (r:pet). Because this index reflects the ratio of rainfall to evaporation, environments that receive rainfall in excess of evaporation (i.e. non-dryland environments) show the greatest variation in the index values. Therefore, r:pet is unlikely to be as suitable for distinguishing between New Zealand's driest environments as average annual water deficit.

3. Average vapour pressure deficit (vpd) in October, which indicates the dryness of the air. Vapour pressure deficit is a measure of water demand that directly indicates the stress experienced by plants as a result of evaporation rate; it indicates the amount of additional water that can be taken up by the air as vapour produced by the evaporation of moisture from plant leaves. This variable was derived using a combination of temperature and humidity estimates, and a model of east–west topographic protection. October is used, since this is the month when westerly winds are the most persistent, resulting in a strong east–west gradient in vapour pressure deficits across New Zealand.

Mapped, landscape-scale predictions of these three different aspects of water balance make it possible to advance understanding of biotic patterns in relation to the availability of moisture across New Zealand, even at sites remote from climate stations. For example, New Zealand's forest tree species vary markedly in abundance, but in different ways, in relation to soil water supply (average annual water deficit) and vapour pressure deficit (Leathwick & Whitehead 2001). However, water availability is only one of many drivers of biotic pattern within New Zealand dryland environments, others being frost, temperature, solar radiation and substrate factors.

3.2 METHODS

3.2.1 Defining the dryland zone

The definition of our dryland zone is necessarily subjective; we made subjective choices on the geographic limits of the zone of interest (New Zealand east of the main axial ranges), the factor(s) used to represent water availability, and the level of water availability used to define degrees of dryness.

To define the dryland zone, we selected the index we judged to best fit patterns of potential vegetation in rain-shadow eastern New Zealand, after comparing the distributions of the three different measures of water balance (Section 3.1) across New Zealand. All of these variables are used in the national LENZ classification of New Zealand environments (Leathwick et al. 2003), but we used average annual water deficit and average monthly water balance ratio variables that are estimated using the FAO-Penman pasture potential evaporation equation, rather than those based on simple potential evaporation that are used in LENZ. This is because FAO-Penman estimates of evaporation are considered to be more accurate in dry environments where water availability is low and variable (Brutsaert 1982; J.R. Leathwick unpubl. data).

Another subjective judgement was required to choose an appropriate cut-off (i.e. upper limit) of water availability to define the outer boundaries of our dryland zone. There were many possible options, from which we selected an explicit biotic indicator: we used the highest water availability value at relict sites of the rare dryland shrub *Muehlenbeckia astonii* as the outer limit of our dryland zone.

3.2.2 Environmental characteristics of the dryland zone

Once we had defined a dryland envelope we used a wide range of environmental variables (40 in total) to distinguish between the types of dryland environment within that envelope (Appendix 1). In addition to the 15 environmental variables that underlie the national LENZ classification, we added a number of other variables that are now available as digital surfaces (i.e. frost, rainfall variability and geology) and are known to be important drivers of biotic pattern within drylands.

Level IV land environments of the LENZ classification (Leathwick et al. 2003) were used as the smallest geographic units in our classification of New Zealand's dryland environments. This allowed boundaries to remain as they are in the national classification, despite these units being grouped somewhat differently.

For each Level IV land environment within our dryland envelope, we calculated the average for each climate and substrate variable, and the percentage area of the 11 classes of top rock geology. We calculated the coefficients of correlation between all pairs of variables across the Level IV land environments. There were strong correlations among the different frost variables and among temperature variables. Several frost variables were strongly correlated, as were those for temperature and solar radiation. We therefore retained only the 29 most independent variables as the basis for our dryland environment classification.

3.2.3 Classification

To identify different types of dryland environments within dry eastern New Zealand, we performed a classification on the table of Level IV land environments by the 29 most independent environmental variables (Appendix 1, Table A1.1), using cluster analysis (city-block distance measure, flexible sorting strategy, with β set to –0.5 to weight the classification towards more even-sized groups; Clifford & Stephenson 1975). We grouped fertility and weatherability substrate factors (acid soluble phosphate, particle size, calcium, induration), following Leathwick et al. (2003); this effectively downweights their contribution to the multivariate analyses by a factor of four. We also grouped five geological substrate classes of minor importance (each accounting for < 1% of the land area, i.e. gneiss, three volcanic rock classes and areas where the influence of underlying mineral material on soil development has been masked by the development of deep peat). Average values for all factors were zero-mean unit-variance transformed for analysis. The classification was terminated at the arbitrary level of eight groups (hereafter 'dryland environmental types') and 40 groups (hereafter 'dryland environmental subtypes').

To describe and compare dryland environmental types and subtypes, we calculated averages for each underlying environmental factor, based on the original data surfaces (Appendix 1, Table A1.2).

3.2.4 Representation in public conservation lands

Using a GIS, we overlaid the latest (September 2003) database of public conservation lands on our dryland classification to determine the area and proportion of each of the dryland environmental types and subtypes represented. We then estimated the areas and proportions of each dryland type represented in DOC-protected areas (by conservancies).

3.3 RESULTS

3.3.1 Defining the dryland zone

Of the three measures of annual water deficit, r:pet (Fig. 1A), Penman (Fig. 1B) and vapour pressure deficit (Fig. 1C), the pattern of annual Penman water deficit (Fig. 1B) provides the best fit with the geographic boundaries of rain-shadow New Zealand east of the main axial ranges, and its isobars correspond well with the boundaries of the relict distribution of *Muehlenbeckia astonii*, which we judge to be an indicator of dryland environments. Leathwick (2001) demonstrated that this variable is correlated with the distribution of forest trees across New Zealand. It distinguishes lowland sites with high to moderate annual water deficits lying in the east of both the North Island and South Island from higher-elevation environments and lowland in the west of both islands that experience negligible annual water deficits (Fig. 1B).

The national distribution of the average monthly water balance ratio (r:pet; Fig. 1A) is similar to that of annual Penman water deficit. However, gradients in moisture balance within dry eastern New Zealand environments are less clearly

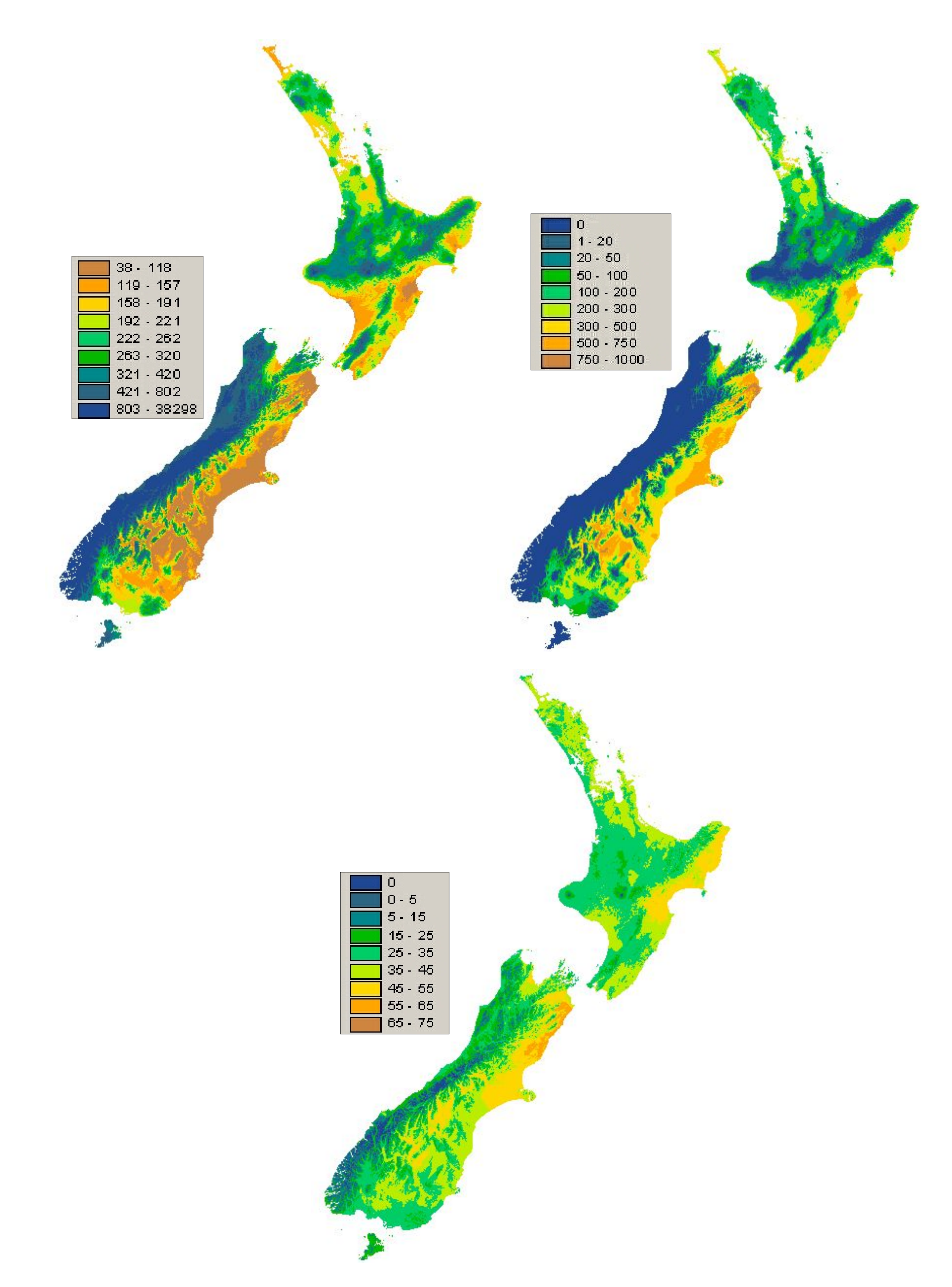

Figure 1. Three measures of water balance across New Zealand. **A**. r:pet = rainfall:FAO-Penman potential evapotranspiration ratio. **B**. Penman deficit (sum of monthly deficits between FAO-Penman potential evapotranspiration and rainfall). **C**. October vapour pressure deficit.

distinguished by the ratio than by the annual Penman water deficit, and the relict distribution of *Muehlenbeckia astonii* corresponded poorly with isobars of r:pet. This is to be expected, since the scale of the r:pet ratio is such that the greatest distinctions are between environments where water is not limiting. For example, r:pet has been shown to correlate well with the national distribution of filmy ferns, which depend upon frequent and reliable rainfall for survival. Nevertheless, the pattern of r:pet indicates that droughts may be experienced across a wide area of New Zealand (e.g. sites as far south as the plains of Southland as well as areas of Northland) in years with lower than average rainfall, even though average annual rainfall exceeds evaporation in these environments.

The highest October vapour pressure deficits are experienced in warm, northeastern South Island and North Island (Fig. 1C). The influence of temperature on this parameter leads to a relatively poor fit with the southeastern portion of the rain-shadow zone.

We therefore chose annual Penman water deficit to define the limits of eastern New Zealand drylands. Within this dryland envelope we included areas lying east of the main axial ranges of both islands with an average Penman deficit of 270 mm or greater, i.e. equivalent to the lowest average Penman deficit across a land environment that presently contains *M. astonii* (Level IV land environment F1.2c, on the coast near Wellington). We excluded a number of areas in the west of the North Island with average Penman deficits of > 270 mm. Coastal parts of the Manawatu, Rangatikei and Wanganui Districts are probably most similar to environments within our eastern dryland envelope, since they are influenced by the rain shadow of South Island mountains. In contrast, the Hauraki Plains, Auckland, Rodney and the Far North District experience warm, high-rainfall subtropical climates.

Within our eastern dryland envelope, we expect that water availability will vary considerably according to substrate and topography at local and regional scales; for example, sites that support *M. astonii* vary from those that are edaphically dry (i.e. dry because of particular soil proerties; in this case, on well-drained greywacke substrates with high proportions of coarse surface rock) to those that are climatically dry but not particularly well drained.

We define a dryland envelope (50 555 km^2; Fig. 2) that accounts for about 19% of New Zealand's total land area (267 297 km^2). It includes all or part of 13 LENZ Level I land environments (Fig. 2). Level I environments N (Eastern South Island Plains, 38%), B (Central Dry Lowlands, 12%), E (Central Dry Foothills, 12%) and Q (South-eastern Hill Country and Mountains, 11%) predominate in terms of land area (Fig. 2). Dryland environments in LENZ Level I A, C, D and G are confined to the North Island, and those in E, K, L, N and Q are confined to the South Island. Areas of the remaining Level I land environments (B, I, F and J) lie on both sides of Cook Strait. The eastern New Zealand dryland zone includes 52 of the 100 Level II environments, and 90 of the 200 Level III environments. It includes > 1 km^2 or all of 181 Level IV land environments, of which 144 lie wholly within the eastern New Zealand dryland envelope.

3.3.2 Eastern New Zealand dryland environments

At the eight-group level, the pattern of dryland environment types is determined largely by latitude (Fig. 3; Appendix 1: Table A1.2). In the north of the dryland zone, mean annual temperature and June solar radiation are high, while July ground frosts are most severe in the south. Subgroups (i.e. the 40 environmental subtypes) may be distinguished by a wider range of factors (however, for brevity, this information is appended in digital form only).

3.3.3 Representation in public conservation lands

Of the DOC conservancies that intersect the dryland zone (see Table 1), Canterbury (39.7%) and Otago (26.0%) contain the largest areas of dryland, while Southland has the smallest area (1.4%).

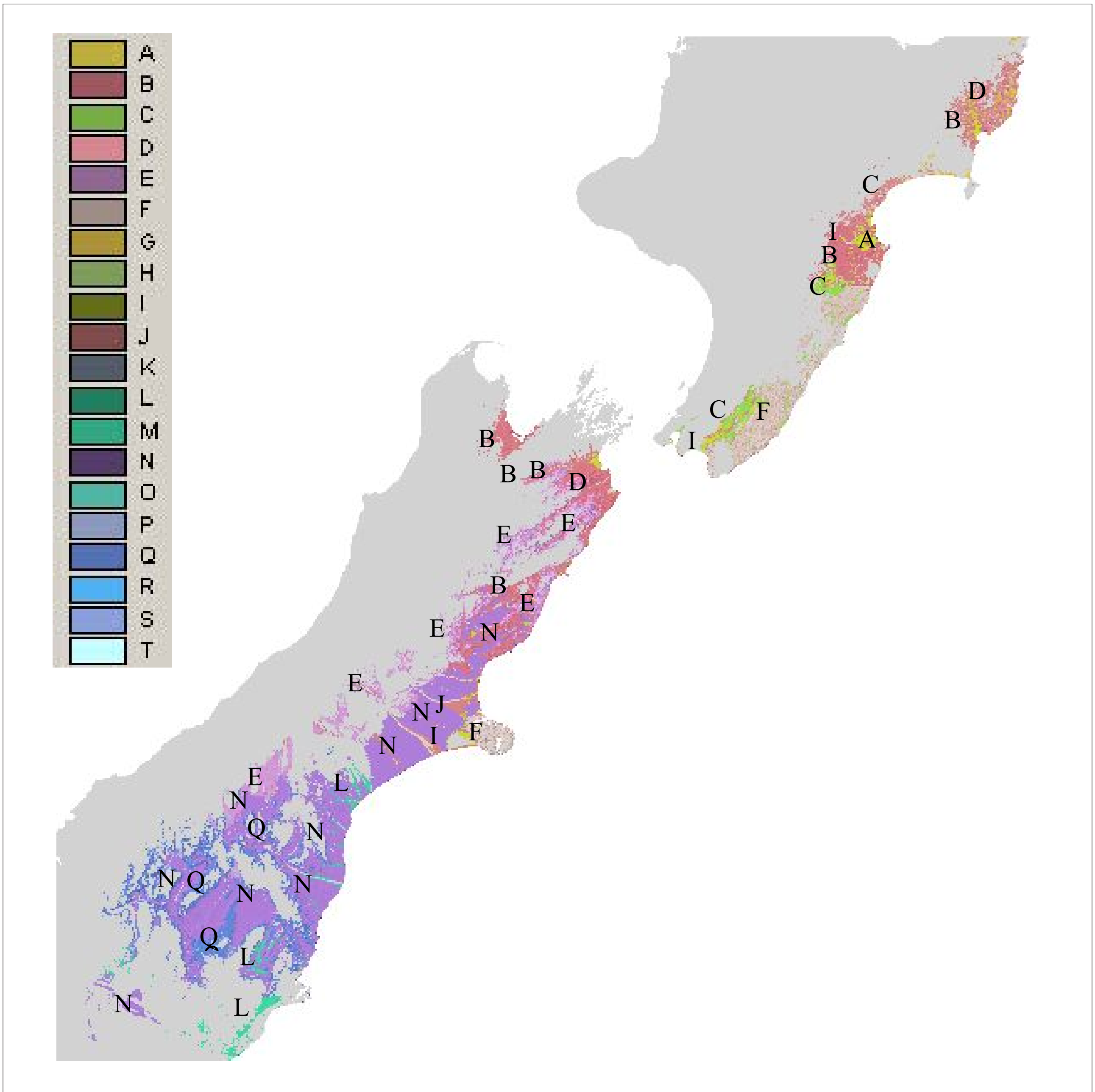

Figure 2. Distribution of LENZ Level I dryland environments within the eastern New Zealand dryland envelope.

Dryland environments are extremely poorly represented in public conservation lands nationally; c. 1.9% of the total land area of the dryland zone is protected. This degree of protection will not be adequate to sustain the full range of biodiversity of New Zealand's dryland ecosystems; for example, the generalised species-area curves suggest that major losses of species result when habitat is reducedbelow c. 20% of original area (Lee & Walker 2004; Walker, Lee et al. 2004c).

Among the conservancies, Nelson-Marlborough has the highest percentage of its dryland land area protected (4.5%), while Hawke's Bay has only 0.4% protected. Of the eight dryland types, type E is the best protected, with almost 5% of its land area currently within public conservation lands. However, less than 1% of dryland types A, B and F are currently protected.

4. Disturbance in pre-settlement dryland ecosystems

4.1 INTRODUCTION

Disturbance drives long-term fluctuations in the structure and functioning of ecosystems. We follow Pickett & White's (1985) definition of disturbance as a relatively discrete event in space and time that alters the structure of populations, communities and ecosystems, and causes changes in resource

TABLE 1. THE DRYLAND ENVIRONMENT IN PUBLIC CONSERVATION LANDS (km^2, %) BY CONSERVANCY AND PERCENTAGE OF THE EIGHT DRYLAND ENVIRONMENTS REPRESENTED IN PUBLIC CONSERVATION LANDS, BY CONSERVANCY.
Dryland area % and protected dryland % represent the percentage that area is of the Eastern New Zealand Dryland Zone.

	EAST COAST	HAWKE'S BAY	WELLINGTON	NELSON-MARLBOROUGH	CANTERBURY	OTAGO	SOUTHLAND	TOTAL
Dryland area	2756 (5.5%)	4463 (8.8%)	3981 (7.9%)	5404 (10.7%)	20074 (39.7%)	13137 (26.0%)	724 (1.4%)	50540 (100%)
Protected dryland	31 (1.1%)	20 (0.4%)	52 (1.3%)	241 (4.5%)	277 (1.4%)	327 (2.5%)	13 (1.7%)	961 (1.9%)
Percentage dryland type protected								
A	0.44	0.33						0.77
B	0.12	0.31	0.43	0.01	0.11	0.00		0.97
C	0.13		0.60	0.38	0.49	0.08		1.68
D				0.98	0.11			1.09
E				3.50	1.30	0.02		4.82
F				0.00	0.48	0.06	0.00	0.54
G				0.03	0.97	0.63	0.07	1.71
H				0.29	0.39	2.46	0.05	3.19
% of Total	0.06	0.04	0.10	0.48	0.55	0.65	0.02	1.90

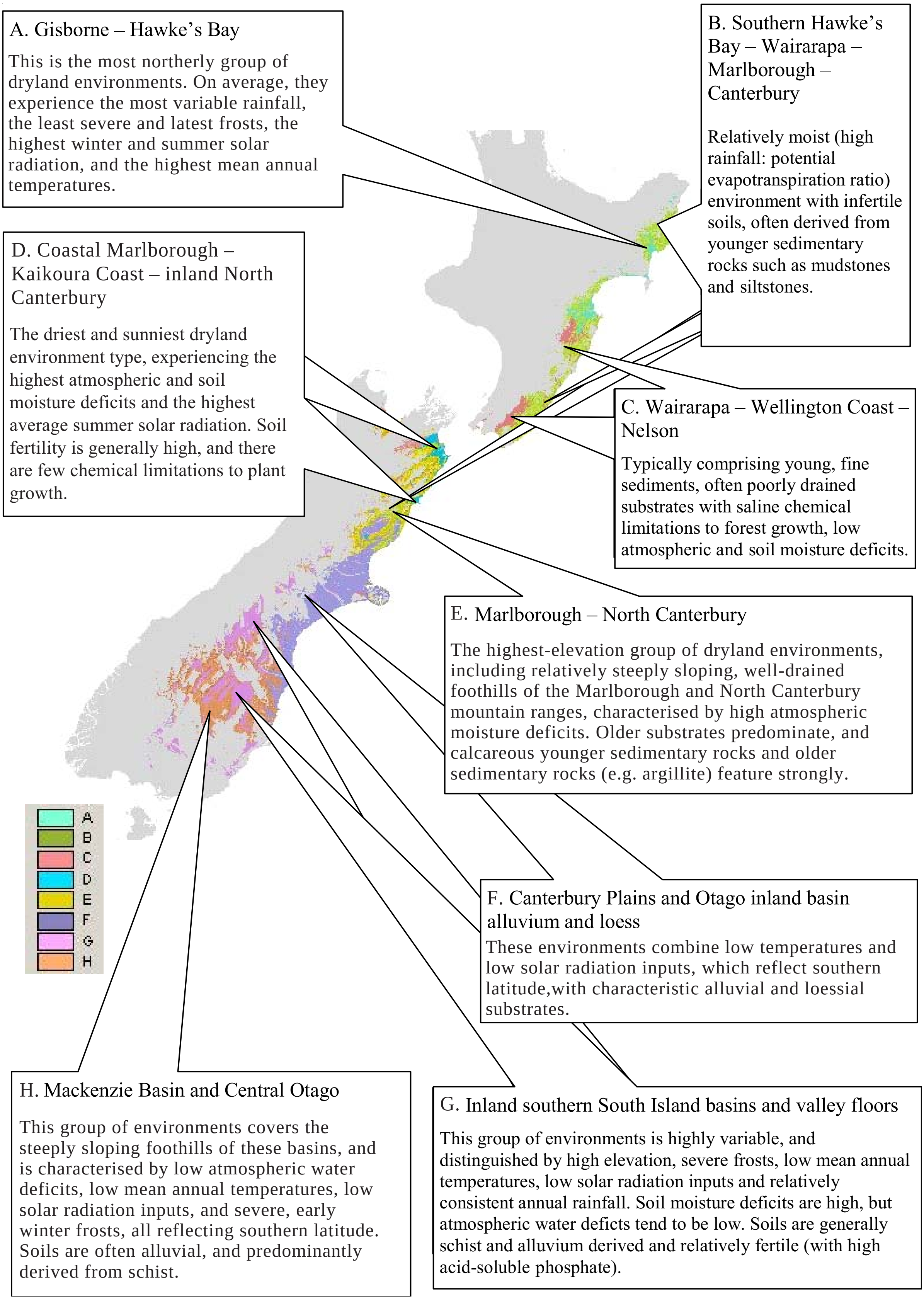

Figure 3. The eight dryland types.

availability or the physical environment. Functionally, disturbance results in reductions in live plant biomass or sudden changes in the cycling of soil organic matter (Chapin et al. 2002).

The term 'disturbance' is difficult to apply unambiguously. Events such as intensive grazing or severe inversion frost seriously disrupt the functioning of some ecosystems, but may be considered 'normal events' in others. Disturbance must therefore be applied in terms of the usual environmental perturbation that is experienced by an ecosystem, and this can be somewhat arbitrary. For example, it can be argued that herbivory is part of the background functioning of ecosystems, whereas stand-killing insect outbreaks are a disturbance. However, because the equivalence of pre- and post-settlement animal impacts in ecosystem processes is a key issue for conservation in eastern New Zealand drylands, we treat herbivory as an agent of disturbance, and examine it in some detail. In contrast, because drought does not alter ecosystem processes, it is not considered to be a disturbance.

The environmental impact of a disturbance process is determined by its mechanical form, geographic scale, periodicity, magnitude and biological effects. Therefore, following Chapin et al. (2002), we considered the effects of different types of disturbance upon ecosystem processes in terms of severity, intensity, size and frequency.

Disturbance **severity** is the magnitude of change in resource supply in the environment. In terms of ecosystem processes, severity is most usefully applied to the quantity of organic matter removed from plants or the soil.

Disturbance **intensity** is the energy released per unit area or time. The intensity of a disturbance often influences the severity of its effect. Intensity and severity may be inversely related. For instance, rapidly moving and intense fires may be less severe than less intense, slow, smouldering fires that consume more fuel (Chapin et al. 2002).

Disturbance **size (scale)** may range from that of a single tree-fall gap to areas of hundreds of square kilometres.

Disturbance **frequency** varies dramatically between ecosystems and disturbance types. Ecosystems are usually most resilient to more frequent (and usually less severe) disturbances (Chapin et al. 2002).

Human activity can modify all four facets of some types of disturbance, but has little effect on other types. For example, flooding and sedimentation regimes may be much modified, while vulcanism is clearly not.

4.2 METHODS

Drawing upon the literature, we subjectively classify the various disturbance phenomena operating in pre-settlement, late Holocene New Zealand under severity, intensity, scale and frequency. This classification is then applied to late Holocene, dryland South Island as a means of considering the relevance and importance of each disturbance mechanism.

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